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A Review of the Taxonomic Structure within Dolly Varden, *Salvelinus malma* (Walbaum 1792), of North America

Examen de la structure taxonomique du Dolly Varden (*Salvelinus malma*) (Walbaum, 1792) en Amérique du Nord

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ABSTRACT

The taxonomic structure within North American Dolly Varden can be recognized by distinguishing subspecies based on criteria put forth by COSEWIC (Committee on the Status of Endangered Wildlife in Canada; see Appendix 1) (2008). After reviewing all available literature, *Salvelinus malma malma* (Walbaum 1792) and *Salvelinus malma lordi* (Günther 1866) can be distinguished as subspecies (designatable units) of *S. malma* based on the COSEWIC criteria. *S. m. malma* range from all north flowing rivers along the Alaska Peninsula north to the Mackenzie River, although they are not present in rivers for approximately 700 km from Point Hope to the Colville River, while *S. m. lordi* range from all south flowing rivers on the Alaska Peninsula south to Washington State. Until further morphological, meristic and genetic analyses are conducted the separation of *S. m. malma* into additional subgroups, such as those proposed by DeCicco and Reist (1999), must wait.

RÉSUMÉ

La structure taxonomique des populations nord-américaines de Dolly Varden peut être observée en distinguant les sous-espèces d'après les critères énoncés par le COSEPAC (Comité sur la situation des espèces en péril au Canada; voir annexe 1) (2008). Après avoir passé en revue l'ensemble de la littérature disponible, on peut désigner *Salvelinus malma malma* (Walbaum, 1792) et *Salvelinus malma lordi* (Günther, 1866) en tant que sous-espèces distinctes (unités désignables) de *S. malma* d'après les critères du COSEPAC. *S. m. malma* est présent dans tous les cours d'eau s'écoulant vers le nord le long de la péninsule de l'Alaska jusqu'au fleuve Mackenzie, bien qu'il soit absent dans les cours d'eau sur environ 700 km de Hope Point jusqu'à la rivière Colville. De son côté, *S. m. lordi* est présent dans tous les cours d'eau s'écoulant vers le sud, de la péninsule de l'Alaska jusqu'à l'État de Washington. Jusqu'à ce que d'autres analyses morphologiques, méristiques et génétiques soient effectuées, le fractionnement de *S. m. malma* en d'autres sous-groupes, comme ceux proposés par DeCicco et Reist (1999), doit être mis en veilleuse.

1.0. INTRODUCTION

The genus *Salvelinus* consists of at least 11 named species to date distributed holarctically (Taylor *et al.* 2001). There has been significant debate surrounding the correct taxonomy of these species due to the great plasticity in morphology, ecology and life history the genus exhibits throughout its range, the stunted populations and color variants that commonly occur, introgression or hybridization that can easily occur between species, and the limited degree of genetic divergence among the taxa because of their recent origin (McPhail 1961; Reist 1989; Grewe *et al.* 1990; Crane *et al.* 1994; Utter and Allendorf 1994). Nelson (1994) recognized three phyletic lines within the genus which he considered to be subgenera namely, *Salvethymus*, containing only one species *S. svetovidovi* (Chereshnev and Skopets 1990) (Long-finned Char) represented by a single population in Lake El'gygytgyn located on the Chukchi Peninsula in north-east Siberia; *Baione* containing two species *S. fontinalis* (Mitchill 1814) (Brook Trout), and *S. namaycush* (Walbaum 1792) (Lake Trout) (both *S. fontinalis* and *S. namaycush* are endemic to North America); and *Salvelinus* which includes all other char in the genus, including the Arctic Char species complex. The Arctic Char complex, which is circumpolar in distribution, includes all remaining members of the genus. There are three (or four) closely related species representing this complex in north-western North America namely: 1) *Salvelinus alpinus* (Linnaeus 1758) (Arctic Char); 2) *Salvelinus malma* (Walbaum 1792) (Dolly Varden); 3) *Salvelinus confluentus* (Suckley 1858) (Bull Trout); and 4) an additional char of uncertain taxonomic status at the species level (see below) *Salvelinus anaktuvukensis* (Morrow 1973) (Angayukaksurak Char), along with one species in Asia *Salvelinus leucomaenis* (Pallas 1814) (Whitespotted Char) (Phillips *et al.* 1995; Reist and Sawatzky 2008). Numerous studies have been conducted over the past 40 years to clarify the relationships among these species including morphological, karyological, and allozyme marker studies, as well as extensive phylogenetic studies using sequences from both mitochondrial and nuclear DNA (Phillips *et al.* 1995; Taylor *et al.* 2001). The results of these studies have clarified specific and subspecific taxonomic boundaries within the genus *Salvelinus*. This report summarizes all available literature to clarify the taxonomic structure within the *S. malma* subgroup based on the COSEWIC criteria for recognizing designatable units (see Appendix 1).

2.0. HISTORY OF THE *S. ALPINUS* COMPLEX

Walters (1955) originally studied the fishes of western Arctic America and eastern Siberia and described the *S. alpinus* complex as "a myriad of forms, described and undescribed.."; he consequently grouped all alpinoid chars under one name, *S. alpinus*, until further studies on the group could be conducted. One of the first publications attempting to distinguish taxonomic structure among the *S. alpinus* complex in North America was McPhail (1961) who used meristic characters and geographical location to distinguish between various groups of fish within the complex. McPhail came to the conclusion that there were two major groups, *S. malma* and *S. alpinus* each with three major forms, a northern, southern and possible interior form in *S. malma*, and an eastern, western Arctic-Bering Sea, and Bristol Bay-Gulf of Alaska form in *S. alpinus*. Additional local forms were also considered possible (McPhail 1961). McPhail's work was widely accepted and applied in subsequent studies, however, limited sampling underestimated both the variation present and the geographic associations of many populations. This interpretation of the *S. alpinus* complex, although accurate to a certain extent, was considered by some (Armstrong and Morrow 1980; Behnke 1980; Craig 1989; Crane *et al.* 1994; Reist *et al.* 1997) to be limited.

McPhail's description included *all* fish found south of the Alaska Peninsula as southern form *S. malma*. Based on a series of osteological, morphometric, and meristic characters studied by Cavender (1978) the southern form Dolly Varden was shown to consist of not one, but two biologically distinct species, *S. malma* (southern form Dolly Varden) and *S. confluentus* (Bull Trout). This led to more extensive research on the relationship between Dolly Varden and Bull Trout (Haas and McPhail 1991; Crane *et al.* 1994; Phillips *et al.* 1994; Leary and Allendorf 1997; Reist *et al.* 2002) which reinforced the distinction of Dolly Varden and Bull Trout as two separate species. These findings were significant because once there was a clear distinction between Dolly Varden and Bull Trout, data from earlier studies in which Bull Trout were mistaken for Dolly Varden had to be re-evaluated.

McPhail's 1961 study also differentiated western Arctic-Bering Sea form Arctic Char and northern form Dolly Varden as two distinct species. McPhail listed all fish from the lower Kuskokwim River north to the Mackenzie River as the western Arctic-Bering Sea form of Arctic Char, with the exception of small populations of fish with higher counts of gill rakers and vertebrae north of the Alaska Peninsula and on the Seward Peninsula, which he classified as northern form Dolly Varden. Morrow (1980) used morphological, meristic and ecological grounds to confirm that the western Arctic-Bering Sea form of Arctic Char and the northern form of Dolly Varden were identical, and therefore represented one species. These findings have been verified by further meristic and genetic analyses and it is now widely accepted that all riverine char west of the Mackenzie River are in fact northern form Dolly Varden (Armstrong and Morrow 1980; Behnke 1980, 1984; Craig 1989; Crane *et al.* 1994; Reist *et al.* 1997). Similar to the above situation for southern Dolly Varden and Bull Trout, once these findings became available information from earlier studies in which these fish were classified as Arctic Char had to be corrected.

Another complexity in understanding the taxonomic structure of the *S. alpinus* species complex occurred when Morrow (1973) named a new species of char, *S. anaktuvukensis* (Angayukaksurak Char), based on morphological and meristic features. This interpretation was short-lived as McCart (1980) showed that *S. anaktuvukensis* was actually an isolated form of Dolly Varden present in the Brooks Range in Alaska, rather than a distinct species. Morrow (1980) agreed and reversed his previous findings. The slight meristic variation found in *S. anaktuvukensis* was attributed to the effects of geographic isolation, which commonly occurs in *S. alpinus*/*S. malma* (McCart and Bain 1974; Bain 1974).

Thus, as a result of these studies, clarifications in the taxonomy of the *S. alpinus* species complex in North America are as follows:

1) Arctic Char is composed of three groups (Behnke 1984) – *S. alpinus alpinus* (Linnaeus 1758); *S. alpinus oquassa* (Girard 1854); and *S. alpinus erythrinus* (Georgi 1775).
2) Bull Trout is composed of two groups (Taylor *et al.* 1999) – A coastal and interior form (not formally named).
3) Dolly Varden is composed of two (Morrow 1980) or possibly three (DeCicco and Reist 1999) groups – a northern form (*S. malma malma* (Walbaum 1792)), a possible intermediate Bering Sea form (not formally named), and a southern form (*S. malma lordi* (Günther 1866)). Also a possible interior form (central inland Alaskan drainages) has been noted (McPhail 1961).

3.0. EVIDENCE OF DESIGNATABLE UNITS IN NORTH AMERICAN DOLLY VARDEN

3.1. TAXONOMY

McPhail (1961) was one of the first to identify both the northern and southern forms of Dolly Varden in north-western North America, although he did not distinguish between the two in terms of nomenclature, and grouped them both under the name *Salvelinus malma*. Also, as noted above, the composition of McPhail's (1961) taxa differed from that of today. Behnke (1980, 1984) named the northern form *S. malma malma* because of its phenotypic similarities, both morphological and meristic, to the original *S. malma malma* found in northeast Asia. He named the southern form Dolly Varden *S. malma lordi* based on one of the first known names applied to the southern form Dolly Varden in North America, *Salmo lordi* (Günther 1866). These names are now widely accepted for both forms and are used respectively from this point forward, and applied retrospectively to the relevant taxa even if the original authors did not do so.

3.2. INHERITED TRAITS

3.2.1. Morphological/Meristic Characteristics

McPhail (1961) first described *S. m. malma* and *S. m. lordi* based almost solely on a series of meristic differences between the two. Most notably he found that *S. m. malma* and *S. m. lordi* differed from each other with respect to the following: the number of gill rakers on the lower limb of the first arch, 11-14 and 8-12 respectively; and the number of vertebrae, 65-71 and 57-66 respectively. McPhail's description of the western Arctic-Bering Sea form of Arctic Char (12-15 gill rakers on the lower limb of the first arch) should be included in his description of *S. m. malma* as they represent the same species. Thus, *S. m. malma* has 11-15 lower gill rakers based upon McPhail (1961). McPhail (1961) also distinguished a distinct inland form with low counts of pyloric caecae in central Alaskan inland drainages. Later studies would both confirm and elaborate on McPhail's findings regarding meristic differences between *S. m. malma* and *S. m. lordi*. *S. m. malma* is characterized by 21-23 gill rakers total, 66-68 vertebrae, and 25-30 pyloric caeca, while *S. m. lordi* is characterized by 16-18 total gill rakers, 62-64 vertebrae, and 20-30 pyloric caeca (Behnke 1980, 1984; DeCicco and Reist 1999). A summary of meristic differences is presented in Table 1. Based on these features, the numbers of gill rakers and/or vertebrae are both reliable distinguishing characteristics between *S. m. malma* and *S. m. lordi*, however, the scope of variation in these characters is poorly known. The number of pyloric caeca is an unreliable distinguishing character due to the broad overlap between both sub-species.

Table 1. Summary of meristic differences between S. m. malma and S. m. lordi. (Behnke 1980, 1984; DeCicco and Reist 1999).

Merisitic Character	*S. m. malma*	*S. m. lordi*
Gill Rakers	21-23	16-18
Vertebrae	66-68	62-64
Pyloric Caeca	25-30	20-30

DeCicco and Reist (1999) proposed two provisional groups within the range of *S. m. malma*, a northern form and an intermediate Bering Sea form. This proposal is based partly on the size distinction that exists between the two populations. Their study showed that Dolly Varden north of the Bering Strait (northern form) grow to a larger size than those to the south (Bering Sea form). Also in an analysis of fish from Norton Sound, Reist *et al.* (1997) found that the fish examined (proposed Bering Sea form) were similar meristically to northern form Dolly Varden, but were similar genetically to southern form Dolly Varden indicating some degree of intermediacy between the two.

3.2.2. Life History

Both *S. m. malma* and *S. m. lordi* exhibit several life history patterns throughout their ranges (Armstrong and Morrow 1980). These life history types include anadromous, riverine (residual), stream-resident (isolated), and lacustrine forms. Life history types and stages are summarized in Sawatzky and Reist (2008).

The anadromous form of *S. m. malma* occurs in stream systems emptying into the Bering, Chukchi, and Beaufort seas, from the north side of the Alaska Peninsula north and east along the coast to the Mackenzie River (although they are not present in rivers for approximately 700 km from Point Hope to the Colville River). As well, a number of apparently anadromous *S. m. malma* have been documented from the interior of Alaska within the Yukon River basin, specifically at the mouth of the Nenana River and in the John River (Armstrong and Morrow 1980). These fish exhibit typical anadromous behaviour, beginning migrations to sea after smoltification between the ages of 3-5, while reaching sexual maturity at 7-9 years of age (Armstrong and Morrow 1980). They leave their natal streams in late June to early July, and return to freshwater in late August or early September to spawn and overwinter. Homing to natal streams is known to occur in spawning and most non-spawning overwintering fish, however, a limited number of non-spawning fish have displayed the ability to stray into non-natal streams to overwinter (Furniss 1975; McCart 1980; Sandstrom and Harwood 2002; Crane *et al.* 2005). All anadromous fish of the northern form appear to return to freshwater at the end of summer sea sojourns. Once sexual maturity is reached individuals usually only spawn every second year (Armstrong and Morrow 1980).

Anadromous *S.m. lordi* occur in stream systems, with or without a lake, that drain into the Pacific Ocean south of the Alaska Peninsula to the Olympic Peninsula in Washington State (Armstrong and Morrow 1980; Taylor *et al.* 2001). Fish that originate from non-lake stream systems first enter the sea as smolts between the ages of 2-4 (Armstrong and Morrow 1980) in two migrations; the first migration takes place in mid-May to early June, while the second migration takes place from September to November. Between July and November these fish enter and leave several freshwater streams in search of a suitable overwintering site (normally a stream system with a lake). Once an appropriate system is found they remain there until the following spring. They may repeat this for a number of years until they reach maturity. Once maturity is reached they return to their natal stream for spawning, and once spent return again to a lake-stream system to overwinter. Fish that originate in lake-stream systems display more typical anadromous behaviour, migrating to sea as smolts between the ages of 3-4 in May and June and returning to their natal lake-stream system before winter. These fish do not enter other freshwater systems before returning to their natal stream. Most anadromous *S. m. lordi* reach maturity between the ages of 4-7, and spawn annually (Armstrong and Morrow 1980).

Both the residual and isolated forms of *S. m. malma* or *S. m. lordi* tend to resemble each other morphologically and thus are different from the respective anadromous form (described above). The residual and isolated forms of both *S. m. malma* and *S. m. lordi* consist of small,

paedomorphic individuals that spend their entire lives in one river system. They retain parr marks and spawning colouration throughout their lives, mature earlier, have slower growth (although rapid growth under the presence of an abundance of food has been shown to increase the proportion of resident fish in some Arctic Char populations (Nordeng 1983), smaller maximum size, lower fecundity, and have shorter life spans than their anadromous counterparts (Armstrong and Morrow 1980; McCart 1980). The residual form occupies the same habitat as anadromous fish throughout the ranges of both *S. m. malma* and *S. m. lordi*, but never migrates to sea, although significant movement within their home rivers between spawning grounds and overwintering sites is exhibited (Armstrong and Morrow 1980). The residual form consists almost exclusively of males, which are believed to spawn with cohabiting anadromous fish following a sneaking strategy typical of salmonids (Bain 1974). Isolated Dolly Varden resemble the residual form but consist of both male and female fish, and are physically isolated in headwater reaches of rivers by barriers such as falls that are impassable to anadromous migrants (Reist *et al.* 2001). Some populations may also be isolated due to distance from marine environments. Isolated fish only spawn with fish from within their own population, however, fish from isolated populations may occasionally contribute individuals to the downstream anadromous populations (Bain 1974; Armstrong and Morrow 1980; McCart 1980; Reist 1989).

Lacustrine *S. m. malma* and *S. m. lordi* do occur within both their respective ranges, although they are less common than either the anadromous or residual/isolated forms. Lacustrine *S.m. malma* have only been documented in one lake, lake CT 28 in the upper Canning River drainage basin, while lacustrine *S.m. lordi* are more widespread (Armstrong and Morrow 1980). All lacustrine Dolly Varden attain larger maximum sizes than other freshwater forms (residual or isolated) due to the wider variety and amount of food available within their habitat. Lacustrine *S. m. malma* apparently do not migrate and live out their entire lives within a lake, whereas lacustrine *S. m. lordi* are usually associated with a stream-lake system. These *S. m. lordi* start out in streams adjacent to a lake, then move into the lake at around two years of age where they live out the remainder of their lives, usually returning to their natal streams to spawn. Populations of *S. m. lordi* have also been found in landlocked lakes, in which they spend their entire lives (Armstrong and Morrow 1980).

As noted previously, DeCicco and Reist (1999) raised the possibility that two sub-groups (northern form and an intermediate Bering Sea form) exist within the range of *S. m. malma* based on morphological and geographic differences, as well as the differences exhibited in their movement patterns, particularly those associated with spawning. Fish found north of the Bering Strait (northern form), particularly in north-western Alaska, most commonly exhibit summer spawning where pre-spawning fish remain in a stream throughout the summer and spawn during August, although along the North Slope of Canada and Alaska this pattern is less common, yet still present. This pattern contrasts to that of fish found in Norton Sound south of the Bering Strait (Bering Sea form) where most pre-spawning fish move directly from the sea to spawning grounds in the late summer or fall (DeCicco and Reist 1999). Furthermore, the Bering Sea form appears to have evolved feeding strategies closely linked to salmon movements. Most of the summer feeding by anadromous Dolly Varden is done at sea, however; when pink salmon (*Oncorhynchus gorbuscha*) are abundant Dolly Varden from Norton Sound often migrate into freshwater to feed on drifting salmon eggs that were not deposited in the gravel. This feeding behaviour is not found in Dolly Varden populations north of the Bering Strait (northern form), even in drainages with large chum salmon (*Oncorhynchus keta*) migrations. These feeding patterns suggest that the putative Bering Sea form may move between fresh and salt water during the summer depending on food availability, while the northern form appears to depend almost exclusively on the marine environment for feeding (DeCicco and Reist 1999).

It should be noted that in this document we are classifying life history type as an inherited trait, but it is still not fully understood whether factors determining specific life history types (i.e., particularly those that determine anadromous and resident forms) are influenced by inherited traits, by the environment, or both (Hendry *et al.* 2004). It is most likely that both the environment, and inherited traits determine life history type in *S. malma* (Reist *et al.* 2001; see Sawatzky and Reist 2008).

3.2.3. Genetic Markers

The divergence of the genus *Salvelinus* within the family Salmonidae was originally thought to have occurred by the late Miocene (12-25 MYBP) based on fossil records (Cavender 1980). Based on mitochondrial DNA (mtDNA) sequence divergence, Grewe *et al.* (1990) determined that the genus *Salvelinus* actually diverged from the rest of the Salmonidae 5-6 MYBP, and that this genus represents a monophyletic group. Furthermore, this mtDNA analysis (Grewe *et al.* 1990) showed that within the *Salvelinus* subgenus, *S. malma* was most closely related to *S. alpinus*, not *S. confluentus*, as was previously thought (Behnke 1980, 1984). These results are congruent with previous studies on chromosomal variation which also show that *S. malma* and *S. alpinus* are the most closely related pair among the *Salvelinus* subgenus (Cavender 1984; Phillips *et al.* 1989). Later studies involving ribosomal DNA (rDNA) analysis (Phillips *et al.* 1994) and allozyme data (Crane *et al.* 1994) indicated the same relationship between *S. malma* and *S. alpinus*. It should also be noted that species distinctness between *S. malma* and *S. alpinus* has been verified by the lack of present day gene flow (hybridization) between the two species, confirmed by studies based on protein electrophoresis (Crane *et al.* 1994; Reist *et al.* 1997; see Reist and Sawatzky 2008).

Early karyological studies revealed considerable differences between *S. m. malma* and S. *m. lordi*. The karyotype (number of chromosomes) of *S. m. lordi* shows a diploid number of 82 (2n=82), while the karyotype of *S. m. malma* shows a diploid number of 78 (2n=78), the same diploid number found in *S. alpinus*. Both species possess chromosome arm numbers of 98 (NF=98) (Cavender and Kimura 1989; Behnke 1989; Phillips *et al.* 1999).

Phylogenetic studies analyzing the ribosomal ITS1 sequences, ND3 gene of the mtDNA, and growth hormone 2 intron C sequences (GH2C) of *S. m. malma* and *S. m. lordi* by Phillips *et al.* (1995, 1999) and Leder and Phillips (1999) support the separation of both as distinct taxa. The ITS1 sequence of *S. m. malma* is closest to *S. alpinus alpinus*, while the ITS1 sequence of *S. m. lordi* is closest to *S. a. erythrinus*. From these data Phillips *et al.* (1999) suggest that *S. m. malma* diverged from *S. a. alpinus* first, then at a later time, *S. m. lordi* diverged from *S. a. erythrinus*. That is, *S. malma* as a species as currently understood is a paraphyletic group. Paraphyly within *S. malma* also supports the designation of *S. m. malma* and *S. m. lordi* as designatable units, but further suggests that *S. m. malma* and *S. m. lordi* may represent distinct species rather than subspecies.

Chromosomal analysis revealed differences in the location of the nuclear organizing regions (NOR) in each form. The NOR is present on a single submetacentric chromosome in *S. m. lordi* (Cavender 1984; Phillips *et al.* 1989) but occurs on a single acrocentric chromosome in a small (n=4) sample of *S. m. malma* (Phillips *et al.* 1999). If verified this difference further supports the recognition of two designatable units corresponding to subspecies in Dolly Varden.

Allozyme data also support the genetic differentiation of *S. m. malma* and *S. m. lordi*. Crane *et al.* (1994) found that a fixed difference at the PEP-LT* locus occurred between *S. m. malma* and *S. m. lordi*. More recently Osinov (2001, 2002) compared allozyme data from different authors

and found support for the genetic differentiation of *S. m. malma* and *S. m. lordi*. He also found that *S. m. malma* has a significantly lower allozyme variability level than do most populations of *S. m. lordi*. Based on his analyses both *S. m. malma* from Asia and North America are placed into one phylogenetic group despite weak genetic divergences among populations. He dismissed the possibility that these divergences represent the division of *S. m. malma* into northern and Beringian subgroups as suggested by DeCicco and Reist (1999) (Osinov 2001, 2002). Rather, he suggests that these slight genetic divergences may be accounted for by the fact that all the populations of *S. m. malma* originated from one ancestral population, which then passed through a "bottleneck" in a glacial refugium, resulting in the slight genetic divergences seen today. Intensive dispersion of *S. m. malma* over its range took place during postglacial times from a single glacial refuge (Osinov 2001, 2002).

Oleinik *et al.* (2005) examined restriction fragment length polymorphisms (RFLPs) of three mtDNA fragments amplified in the polymerase chain reaction (PCR). This study found three phylogenetic groups of mtDNA haplotypes which reflect the existence of three discrete subspecies in the Pacific Basin, *S. m. malma*, *S. m. lordi*, and *S. m. krascheninnikovi* (Asian southern form Dolly Varden). These findings were congruent with those of Osinov (2001, 2002), in that all northern form Dolly Varden form one group exhibiting low genetic differentiation, and that this group originated from one refugium that dispersed post-glacially. It was also found that *S. m. lordi* was more closely related to *S. m. malma* than to *S. m. krascheninnikovi*.

3.3. GEOGRAPHIC RANGES

As mentioned previously the exact geographic ranges of the northern and southern forms of Dolly Varden are difficult to determine due to prior confusion with, and misidentification as, either *S. alpinus* or *S. confluentus* (however, see Sawatzky and Reist 2008). McPhail (1961) originally described the distribution of *S. malma* as ranging from northern California to the lower Kuskokwim River, Alaska, with a few populations to the north (of the Alaska Peninsula) and on the Seward Peninsula (Figures 1 and 2). This was refined once studies clearly identified the existence of *S. m. malma*, *S. m. lordi*, and *S. confluentus* as distinct species and re-aligned the content of the respective taxa (Cavender 1978; Behnke 1980, 1984; Morrow 1980; Armstrong and Morrow 1980; Craig 1989; Haas and McPhail 1991; Crane *et al.* 1994; Phillips *et al.* 1994; Reist *et al.* 1997; Leary and Allendorf 1997; DeCicco and Reist 1999; Redenbach and Taylor 2002; Reist *et al.* 2002; Sawatzky and Reist 2008). This revised distribution has *S. m. malma* present in all north flowing rivers along the Alaska Peninsula north to Point Hope, then absent for approximately 700 km along the coastal plains of the central North Slope due to a lack of suitable habitat. The distribution of *S. m. malma* then continues from the Colville River east to the Mackenzie River. The range of *S. m. lordi* was also clarified to include all south flowing rivers on the Alaska Peninsula south to Washington State. This is widely accepted for both forms of Dolly Varden, although DeCicco and Reist (1999) further tentatively divided the range of *S. m. malma* into two groups. All fish north of the Bering Strait east to the Mackenzie River encompass the northern form of *S. m. malma*, while the intermediate Bering Sea form ranges from the Bering Strait south to the northward draining rivers of the Alaska Peninsula (Figure 3). This represents our best understanding of the Dolly Varden's distribution in North America at present, but is subject to change as more information becomes available.

Taylor *et al.* (1999) and Armstrong and Morrow (1980) documented both anadromous and stream-resident Dolly Varden far inland in central Alaska (Figure 3), however, neither conducted in-depth analyses of morphological, meristic, or genetic characters. Therefore, whether or not these fish represent another unique form of Dolly Varden (interior form) as suggested by McPhail (1961) remains unresolved at present. Additional research conducted on fish from this

area is required. Current available data classifies all Dolly Varden north of the Alaska Peninsula as *S. m. malma*.

4.0. SUMMARY

After reviewing the available literature it is clear that *S. m. malma* and *S. m. lordi* should be considered two distinct subspecies in North America based upon the COSEWIC criteria for recognizing designatable units. *S. m. malma* and *S. m. lordi* are both separate taxa currently recognized by relevant scientific authorities, are genetically distinct in terms of both inherited traits and genetic markers, and display disjunction across their geographic ranges. Thus, two taxa, *S. m. malma* and *S. m. lordi*, formally recognized at present as subspecies within North American Dolly Varden appear to be fully justified. Using the highlands and drainage patterns of the Alaska Peninsula as the logical demarcation, southern Dolly Varden (*S. m. lordi*) is distributed in Pacific Ocean drainages from Pacific drainages on the Alaska Peninsula southwards into British Columbia and northern Washington State. Northern Dolly Varden (*S. m. malma*) is distributed in Bering Sea, Chukchi Sea and Beaufort Sea drainages from Bering Sea drainages on the Alaska Peninsula northwards to Point Hope, then absent for approximately 700 km along the coastal plains of the central North Slope, with its distribution then continuing from the Colville River east to the Mackenzie River. The further separation of *S. m. malma* into distinct subgroups, as proposed by DeCicco and Reist (1999) and McPhail (1961), can not be justified until ongoing morphological, meristic and genetic analyses are completed.

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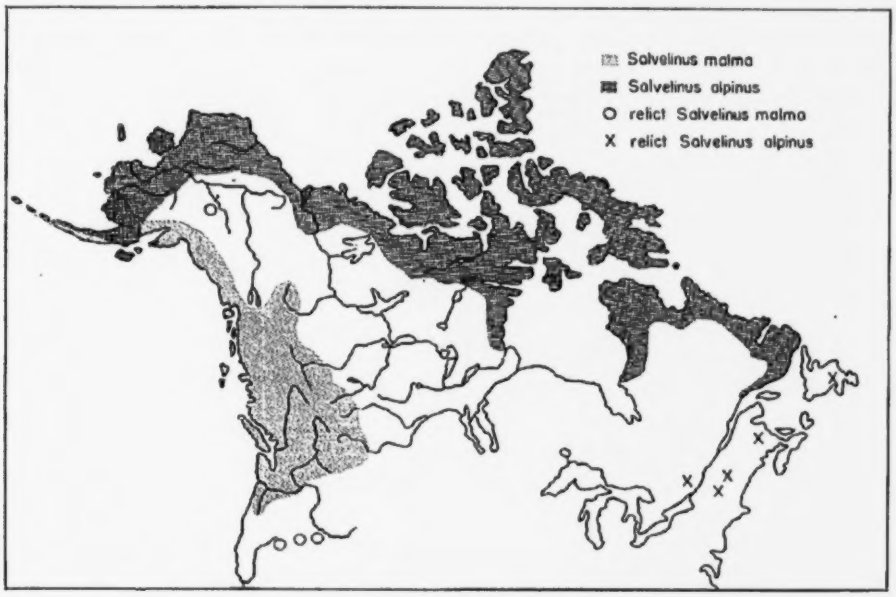

Figure 1. Distribution of S. alpinus *and* S. malma *according to McPhail (1961).*

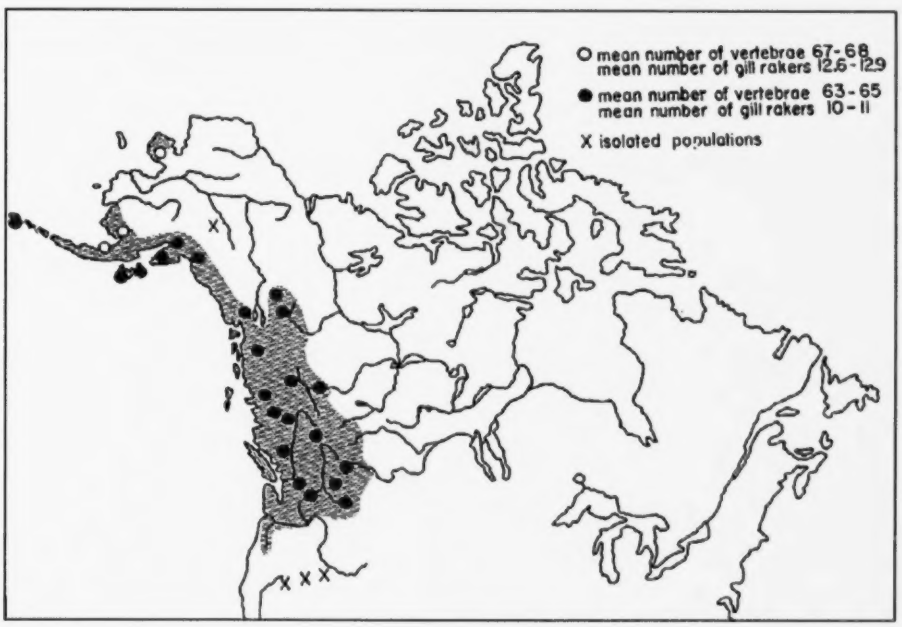
O mean number of vertebrae 67-68
mean number of gill rakers 12.6-12.9
● mean number of vertebrae 63-65
mean number of gill rakers 10-11
X isolated populations

Figure 2. Distribution of northern (open circles) and southern (filled circles) form Dolly Varden according to McPhail (1961).

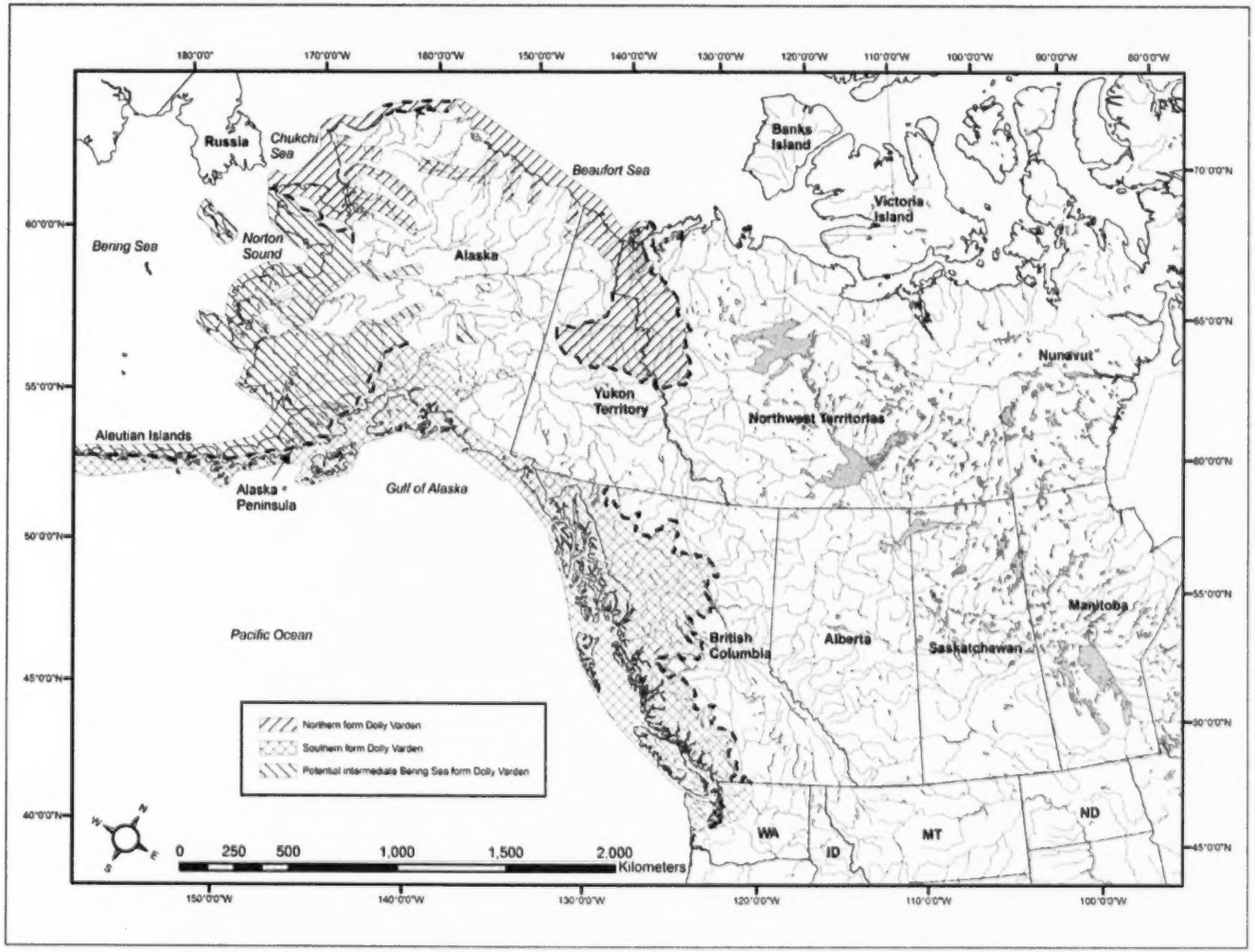

Figure 3. Most recent distribution of S. m. malma *and* S. m. lordi *with the Bering Sea "Intermediate" form of* S. m. malma *included (Sawatzky and Reist 2008 and references therein). Dashed lines indicate uncertainty in extent of distribution. The northern form taxonomically includes both the true northern form and the putative Bering Sea form.*

APPENDIX 1

COSEWIC GUIDELINES FOR THE IDENTIFICATION OF DESIGNATABLE UNITS
Approved November 2009

COSEWIC may assess designatable units (DUs) when a single status designation is thought not to reflect the probability of extinction of a wildlife species.

Designatable units should be discrete and evolutionarily significant units of the taxonomic species, where "significant" means that the unit is important to the evolutionary legacy of the wildlife species as a whole and if lost would likely not be replaced through natural dispersion.

Following is a set of guidelines to assist in the identification of DUs for the purpose of status assessment by COSEWIC. The guidelines should be seen as aids for identifying DUs and not as rigid criteria.

1) Subspecies or Varieties:

A unit may be recognized as a DU if it represents a named subspecies or variety identified in accordance with COSEWIC's guidelines for naming subspecies and varieties. COSEWIC may choose not to recognize a named subspecies or variety as a DU if current scientific data do not support its validity.

2) Discrete and Evolutionarily Significant Populations:

A population or group of populations may be recognized as a DU if it has attributes that make it "discrete" and evolutionarily "significant" relative to other populations.

The first step in identifying DUs is to ask whether the population or group of populations is discrete from other populations.

Discreteness:

A population or group of populations may be considered discrete based on one or more of the following criteria:

1. Evidence of genetic distinctiveness including, but not limited to, inherited traits (e.g. morphology, life history, behaviour) and/or neutral genetic markers (e.g., allozymes, DNA microsatelites, DNA restriction fragment length polymorphisms (RFLPs), DNA sequences).

2. Natural disjunction between substantial portions of the wildlife species' geographic range, such that movement of individuals between separated regions has been severely limited for an extended period of time and is not likely in the foreseeable future and where the disjunction is likely to favour the evolution of local adaptations.

3. Occupation of differing eco-geographic regions that are relevant to the wildlife species and reflect historical or genetic distinction, as may be depicted on an appropriate ecozone or biogeographic zone map. Some dispersal may occur between regions, but it is insufficient to prevent local adaptation.

Significance:

If a population or group of populations is considered discrete, based on one or more of the above criteria, then its significance may next be considered. A population may be considered significant based on, but not limited to, one or more of the following criteria, each of which can be considered a measure of evolutionary significance.

1. Evidence that the discrete population or group of populations differs markedly from others in genetic characteristics thought to reflect relatively deep intraspecific phylogenetic divergence. Such differences would typically be manifested as qualitative genetic differences at relatively slow-evolving markers (e.g., fixed differences in mitochondrial or nuclear DNA sequences or fixed differences in alleles at multiple nuclear loci). Quantitative (frequency) differences of shared alleles, especially for rapidly-evolving markers such as microsatellites, generally would not be sufficient to meet this criterion.

2. Persistence of the discrete population or group of populations in an ecological setting unusual or unique to the wildlife species, such that it is likely or known to have given rise to local adaptations.

3. Evidence that the discrete population or group of populations represents the only surviving natural occurrence of a wildlife species that is more abundant elsewhere as an introduced population outside of its historical range.

4. Evidence that the loss of the discrete population or group of populations would result in an extensive gap in the range of the wildlife species in Canada.

It is important to recognize that some criteria provide more compelling evidence of "discreteness" and "significance" than others; hence, when identifying a DU, it is important to present the best available evidence for all criteria that are met.